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Revision of the subterranean amphipod genus *Spelaeogammarus* (Bogidiellidae) from Brazil, including descriptions of three new species and considerations of their phylogeny and biogeography

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Abstract.—Three new subterranean amphipods of the genus *Spelaeogammarus* da Silva Brum, 1975, are described from eastern Brazil, bringing the total number of species in the genus to four. Based on the examination of type-material of *Spelaeogammarus bahiensis,* a comparative diagnosis of all four species of *Spelaeogammarus,* including the new species *Spelaeogammarus spinilacertus, Spelaeogammarus trajanoae,* and *Spelaeogammarus santanensis,* is given. A diagnosis for the genus is also provided. The occurrence of these species in caves that are separated from each other in discontinuous karst areas is biogeographically significant for the family Bogidiellidae in continental South America.

Exploration of caves in eastern Brazil in the early 1970s resulted in the discovery of the new bogidiellid genus and species *Spelaeogammarus bahiensis* (da Silva Brum, 1975). The specimens were collected from a cave near Curaçá, capital of the district Matamuté, in the state of Bahia. Subsequently, between 1989 and 1993, many additional specimens from various caves in Bahia were collected by Brazilian speleologists and sent to us for identification. Because these specimens differed morphologically from the description of *Spelaeogammarus bahiensis,* we borrowed paratypes of this species from the Museu Nacional in Rio de Janeiro, for a comparison with the new material. The paratypes enabled us to identify and describe three new species and also to diagnose the genus *Spelaeogammarus.* In addition, a key to the four species of the genus is provided as well as a table detailing morphological differences.

The holotypes of the new species are deposited in the Museu Nacional in Rio de Janeiro (MNRJ), Brazil, as indicated.

Genus *Spelaeogammarus* da Silva Brum, 1975

Spelaeogammarus da Silva Brum, 1975: 125–128.

Type species (by monotypy): *Spelaeogammarus bahiensis* da Silva Brum, 1975.

Diagnosis.—Eyes absent. Body smooth, unpigmented. Coxal plates 1–2 small, wider than long; plates 3–6 longer than wide, overlapping. Antenna 1 about 45–50% of body length, primary flagellum longer than peduncle, with 16–20 segments. Accessory flagellum with 4–5 segments. Antenna 2 flagellum bearing 7–10 segments. Mandibular palp 3-segmented. Maxilla 1 with symmetrical, 2-segmented palp; inner plate with 3 plumose setae; outer plate bearing 6–7 serrate spines. Inner plate of maxilliped bearing apically 2 bifid (y-shaped) spines; outer plate with 3 or 4 blade-like spines apically and subapically. Propodus of gnathopod 1 larger than that of gnathopod 2. Dactyls of both gnathopods distinctly serrate along inner margins. Pereopods without any trace of lenticular organs; pereopods 5–7

Table 1.—Major morphological differences of the four species of the genus *Spelaeogammarus*.

Character	*S. spinilacertus*	*S. trajanoae*	*S. santanensis*	*S. bahiensis*
Accessory flagellum	4 segments	4 segments	5 segments	4 segments
Antenna 2 flagellum	7 segments	7 segments	8–10 segments	7 segments
Maxilla 1: outer lobe	6 serrate spines + 1 plumose seta	6 serrate spines + 1 plumose seta	7 serrate spines	7 serrate spines
Maxilliped: apical margin of inner lobe	4 plumose setae	4 plumose setae	2 plumose setae	no plumose setae
Gnathopod 1	propod a littler larger than basis	propod a littler larger than basis	propod much larger than basis	propod a littler larger than basis
Gnathopod 1: post. margin of basis	6–8 setae (some double)	9–10 setae (all single)	~20 setae (all single)	7–9 setae (all single)
Gnathopod 1: ant. margin of basis	2–4 spines + 1 short seta	5–9 short setae	4 short setae	3–5 short setae
Gnathopod 2: post. margin of basis	9–10 setae	8–9 setae	21–23 setae	~9 setae
Coxal plate 5	1 spine + 9 setae	1 spine + 17–18 setae	1 spine + 12 setae	1 spine + 20–21 setae
Coxal plate 6	1 spine, no setae	1 spine, no setae	1 spine + 1 seta	1 spine + 20–21 setae
Pleopods: inner ramus	4–5 setae	5–7 setae	7–8 setae	~7 setae
Uropod 3: outer ramus	~20 bifurcate setae	~20 bifurcate setae	~8 bifurcate setae	missing
Telson: spines per lobe	2 apical + 3–4 subapical	3 apical + 2–3 subapical	1 apical + 3 subapical	2 apical + 3–4 subapical

bases broad, propodus and/or carpus with long, bifurcate setae. Pleopods and uropods unmodified. Pleopods biramous, with 3-segmented outer ramus and 1-segmented inner ramus, rami subequal in length. Uropods biramous: peduncle of uropod 1 with 3 or 4 large basiofacial (ventrolateral) spines; uropod 3 with subequal, 1-segmented rami, outer ramus bearing a row of long, bifurcate setae along medial margin. Telson typically longer than wide, apex with shallow excavation, bearing apical and subapical spines. Coxal gills present on pereopods 4–6. Oostegites linear and elongate, on pereopods 2–5. No sexual dimorphism in any characters.

Key to the species of *Spelaeogammarus* (based on males and females)

1. Accessory flagellum of antenna 1 with 4 segments; flagellum of antenna 2 with 7 segments; propodus of gnathopod 1 slightly larger than basis 2

   Accessory flagellum of antenna 1 with 5 segments; flagellum of antenna 2 with 8–10 segments; propodus of gnathopod 1 much larger than basis ..... *S. santanensis*
2. Coxal plate 6 bearing 1 spine, setae absent; outer plate of maxilla 1 with 6 serrate spines and 1 plumose seta; inner plate of maxilliped with 4 plumose setae 3

   Coxal plate 6 bearing 1 spine and about 20 setae; outer plate of maxilla 1 with 7 serrate spines; inner plate of maxilliped without plumose setae ..... *S. bahiensis*
3. Anterior margin of basis of gnathopod 1 with 5–9 short setae; coxal plate 5 bearing 1 spine and 17–18 setae ..... *S. trajanoae*

   Anterior margin of basis of gnathopod 1 with 2–4 spines (or longer setae) and 1 short seta; coxal plate 5 bearing 1 spine and about 9 setae ..... *S. spinilacertus*

Spelaeogammarus spinilacertus, new species
Figs. 1–5, 6c

Material examined.—Estado do Bahia, Brazil: holotype male (6.1 mm) and 1 paratype male (7.5 mm) from Baixa do Salitre Cave, Iraquara, collected by J. A. Cardoso, Sep 1993; 4 paratypes (3 females, 1 male) from Baixa do Salitre Cave, collected by L. Mendes & E. Rubbioli, 24 May, 1997; allotype female (8.1 mm) and 2 paratypes (1 male, 1 female), from Jaburu Cave, Iraquara, collected by J. A. Cardoso, Sep 1993.

The holotype and allotype are dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13340) and allotype are deposited in the Museu Nacional. The remaining 7 paratypes are retained in the research collection of the second author.

Diagnosis.—*Spelaeogammarus spinilacertus* is easily distinguished from other species in the genus by 2–4 spines or setae of corresponding length on the distoanterior margin of basis of gnathopod 1. Largest male 10.5 mm, largest female 10 mm.

Description.—Antenna 1 (Fig. 2a) about 45–50% of body length. Peduncular segments 1–3 gradually decreasing in length; peduncular segment 1 with 3–4 spines; peduncular segment 2 with 2–3 short spines; peduncular segment 3 bearing 0–2 spines. Primary flagellum longer than peduncle, with 17–20 segments; aesthetascs on most segments; accessory flagellum with 4 segments, terminal segment vestigial.

Antenna 2 (Fig. 2b) about 85% length of antenna 1. Peduncular segment 4 longer than peduncular segment 5; peduncular segment 5 with 3–4 ventral and 2–4 medial spines. Flagellum with 7 segments, 1st segment twice as long as average length of segments 2–6.

Upper lip (Fig. 2c) as long as broad, trapezoidal, with few apical setules.

Mandible (Fig. 2h, i): Palp 3-segmented, with 3–4 terminal setae; 2nd segment bearing 2 apical and 2–3 subapical setae. Molar rounded and well developed, with 1 long lateral seta. Both incisor and lacinia mobilis on left mandible with 5 irregular, rounded cusps (Fig. 2h); 3 long and 3 short plumose spines between lacinia and molar. Right mandible (Fig. 2i): lacinia apically serrated,

consisting of irregularly pointed denticles; 2 long and 2 short plumose spines between lacinia and molar.

Lower lip (Fig. 2d) bearing setules on outer lobes, outer and mandibular lobes with rounded corners.

Maxilla 1 (Fig. 2e): Palp 2-segmented, with 5–6 apical setae and few lateral setules. Outer plate with 6 serrate spines and 1 plumose spine; inner plate with 3 plumose setae.

Maxilla 2 (Fig. 2f): Outer plate apically with 1–2 comb-like setae, ±15 medium-sized plumose setae and 2 large plumose spines (slightly subapical); medial margin with few fine setules; apical margin of inner plate bearing ±18 long comb-like setae and ±5 short naked setae (seta/spine types in Fig. 2g).

Maxilliped (Fig. 2j, 6c): Segment 1 of palp with 1–2 medial setae; segment 2 bearing 12–13 medial setae; dactyl long and slender, bearing a row of marginal setules. Inner plates apparently fused along medial margins.

Gnathopod 1 (Fig. 3a): Posterior margin of basis with 6–8 long setae (some doubly inserted); anterior margin bearing 2–4 spines plus 1 short seta. Carpus with 8 setae on posterior lobe (4–6 comb-like and 2–3 naked). Propodus ovate, almost twice as long as broad, larger than gnathopod 2 propodus; palm uneven, serrate with minute setules at corner (Fig. 3b); palmar margin bearing 7–8 normal spines and 15–19 short bifid spines on lateral margin; medial margin with 6 short setae, 1 normal angular spine, and 4–6 oblique subangular spines (1–2 relatively long). Dactyl about 70% length of propodus; inner margin with distinct row of denticles (Fig. 3c).

Gnathopod 2 (Fig. 3d): Posterior margin of basis bearing 9–10 long setae. Carpus posteriorly with fine setules and 7 sets of setae (1–5 setae per set). Propodus ovate, almost twice as long as broad; palm oblique, with 5–6 corner spines (Fig. 3e), 11–14 short lateral bifid spines, and 7–8 short medial setae; palmar margin finely serrate at whole margin, with minute setules at corner. Dactyl about 50% length of propodus; inner margin with distinct row of denticles.

Pereopods 3 and 4 subequal (Fig. 4a). Basis without spines, anterodistal margin even (pereopod 4 basis with 0–1 spine plus 1 seta at anterodistal margin). Posterior margin of carpus bearing 4–5 spines. Propodus with 8–9 spines along posterior margin and 2 apical spines. Dactyl about 24% length of propodus (Fig. 4b).

Pereopod 5 (Fig. 4c): Basis with 10–11 spines at posterior margin (distal and proximal group of spines separated by a gap); anterior margin bearing 13–15 spines; anterior lateral surface with 6 short setae; 10–11 short setae at posterior margin and posterior lateral surface. Ischium with 1 spine and 3 setae. Anterior margin of carpus with a row of long, bifurcate setae (Fig. 4f) and 6–12 spines (some doubly inserted). Propodus anteriorly with a row of long, bifurcate setae, occurring progressively shorter distally, with slightly thicker bases; lateral margin with 17–19 spines (some doubly inserted); proximal part with 3–4 spines. Dactyl 14–20% length of propodus.

Pereopod 6 subequal to pereopod 5 but slightly longer.

Pereopod 7 (Fig. 4d): Basis ovate, bearing 8 spines on anterior margin and 7–9 spines on posterior margin. Ischium with 2 spines. Merus with 3 spines on posterior margin and 5 spines at anterior margin (1 singly and 2 doubly inserted). Carpus with 13 spines, occurring in 6–7 sets (with 1–3 spines per set) on anterior margin, 4 spines (2 doubly inserted) plus 4 setae on posterior margin, and 10–11 terminal spines. Propodus bearing 12 slender spines on anterior margin and rows of long, bifurcate setae along posterior and anterior margins (Fig. 4f). Dactyl about 27% length of propodus.

Pereopods 1–7 without any trace of lenticular organs; pereopods 5–7 with broad bases.

Coxal gills ovate, present on pereopods 4–6.

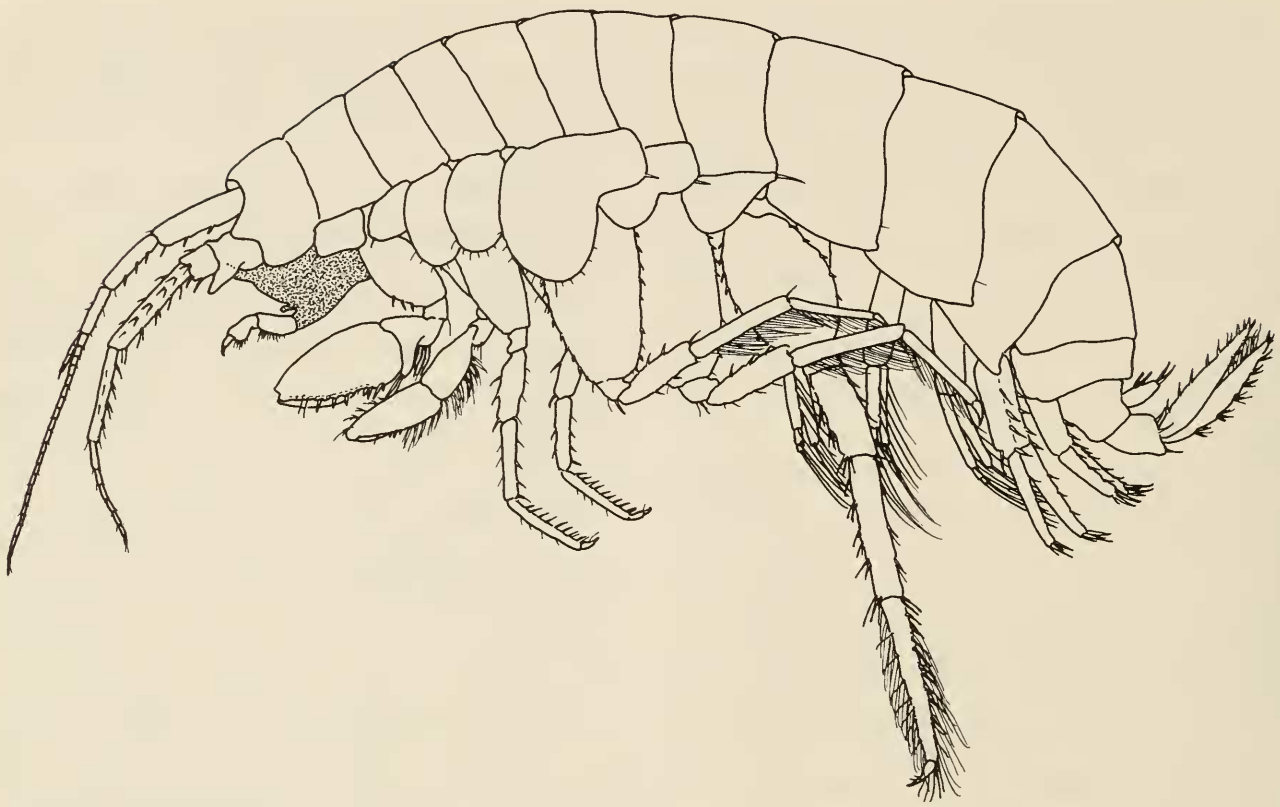

Fig. 1. *Spelaeogammarus spinilacertus* n. sp., allotype female (8.1 mm) from Jaburu Cave, Estado do Bahia, Brazil.

Coxal plates 1 and 2 (Fig. 3f, g) about equal in size, subrectangular to ovate in shape, wider than long; plates 3–6 longer than wide, overlapping; plates 3 and 4 about the same size, plate 5 largest; plate 5 and 6 with distinct anterodistal lobes (Fig. 4c, g); plate 7 (Fig. 4e) subtriangular to irregular in shape, with single long spine at tapered posterior corner.

Oostegites linear and elongate, on pereopods 2–5.

Pleopods 1–3 morphologically alike (Fig. 5a), decreasing slightly in size posteriorly, with subequal outer and inner rami. Outer rami 3-segmented, with 2 terminal plumose setae per segment; segment 1 bearing 6–10 lateral plumose setae and 5–8 medial plumose setae. Inner rami 1-segmented, with 4–5 medial plumose setae.

Epimeral (pleonal) plates subquadrate, with small, subacute posterior margins, bearing 1 setule each (Fig. 4h).

Uropod 1 (Fig. 5b): Rami subequal in length, slightly shorter than peduncle. Peduncle with 3 spines on dorsolateral, dorsomedial, ventrolateral (basofacial), and apical margin, respectively. Outer ramus bearing 3–4 dorsolateral and 4 apical spines. Inner ramus with 5 apical and 4–5 dorsolateral spines, the latter occurring as 3–4 singly and 1–2 doubly inserted.

Uropod 2 (Fig. 5c): Peduncle bearing 1 dorsomedial spine, 2 dorsolateral spines, and 2 apical spines. Outer ramus slightly shorter than inner ramus, as long as peduncle, bearing 2–3 spines dorsolaterally and 4 spines apically. Inner ramus with 5 dorsolateral and 4–5 apical spines.

Uropod 3 (Fig. 5d) with subequal, lanceolate rami, both 1-segmented. Peduncle about 46% length of rami, with 2 apical spines, 1 subapical spine, and 1 small dorsoproximal spine. Outer ramus bearing 3 apical spines, 6 sets of spines (with 2–3 spines per set) along lateral margin, and about 20 bifurcate long setae along medial margin (Fig. 5e). Inner ramus with 3 apical spines; lateral margin with 5 spines; medial margin bearing 9 spines (some doubly inserted).

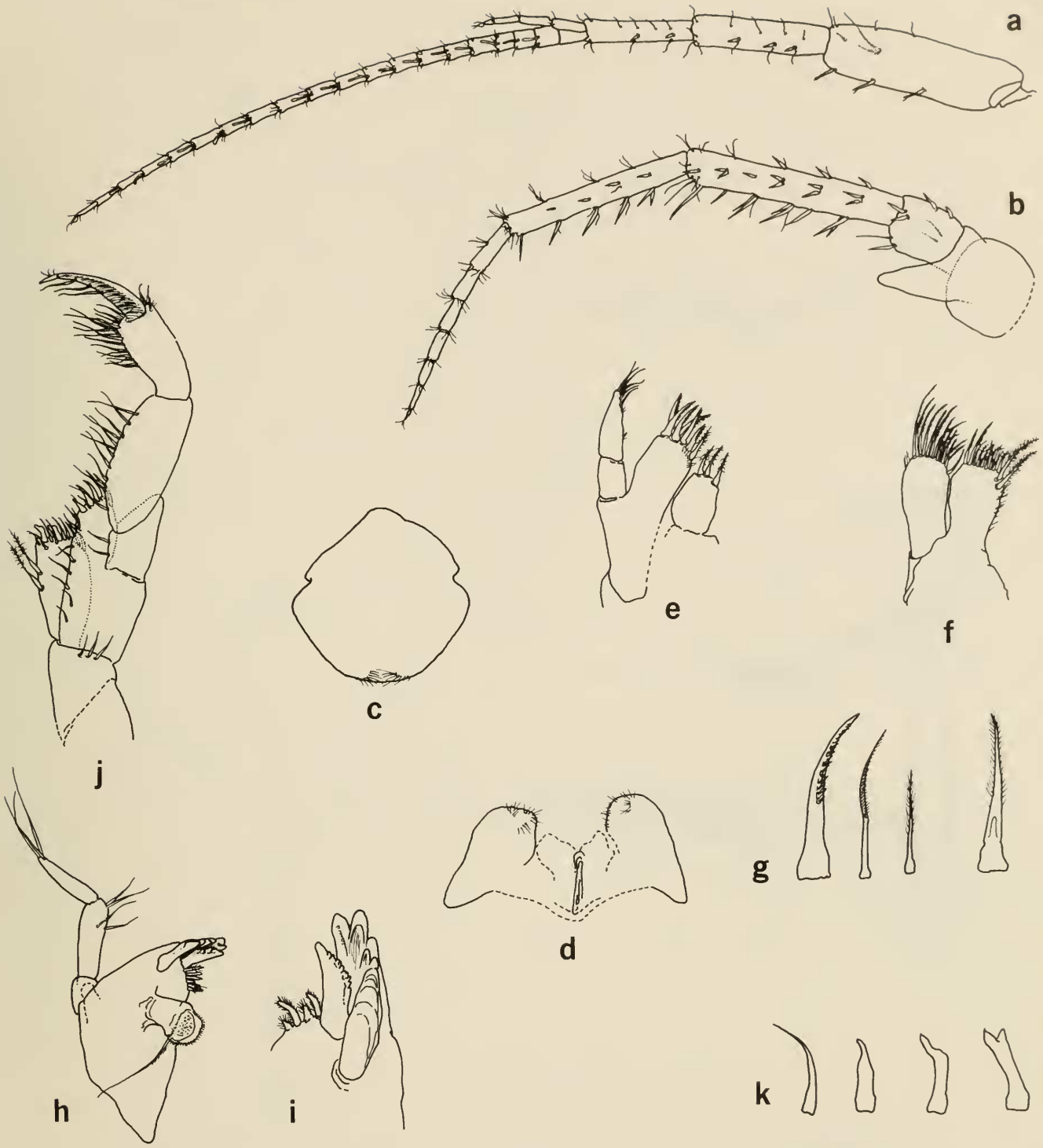

Fig. 2. *Spelaeogammarus spinilacertus* n. sp., allotype female: a) antenna 1, b) antenna 2, c) upper lip, d) lower lip, e) maxilla 1, f) maxilla 2, g) spine and seta types (on maxilla 1 and 2, maxilliped, and gnathopod 1 and 2), from left: serrate spine, comb-like seta, plumose seta, and plumose spine, h) left mandible, i) right incisor and lacinia mobilis, j) maxilliped, k) spine types of maxilliped outer plate (far left 2) and inner plate (far right 2).

Telson (Fig. 5f) width about 84% of length, with shallow excavation (10% of length); each side bearing 3 setae, 2 apical and 2 (sometimes 3) subapical spines.

Etymology.—The epithet *spinilacertus* is a noun in apposition, alluding to the presence of spines on the anterior margin of the basis of gnathopod 1. It is formed by combining *spini,* from Latin meaning thorn or spine, with *lacertus,* from Latin meaning upper arm (~basis).

Remarks.—Two of the three specimens

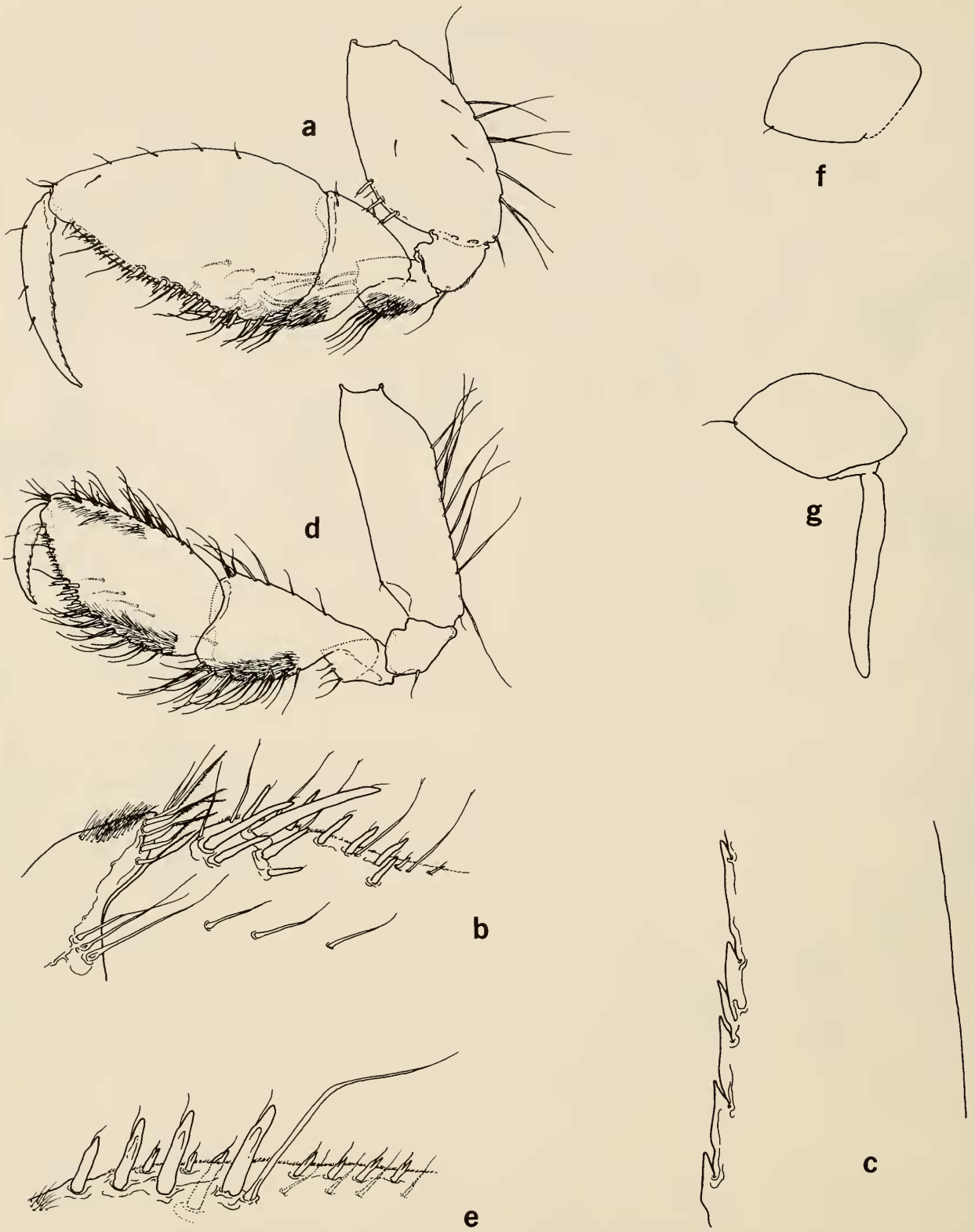

Fig. 3. *Spelaeogammarus spinilacertus* n. sp., holotype male: a) left gnathopod 1, b) detail of right gnathopod 1, c) detail of right gnathopod 1 dactyl, d) left gnathopod 2, e) detail of left gnathopod 2; allotype female: f) coxal plate of gnathopod 1, g) coxal plate of gnathopod 2.

from Jaburu cave showed variation in some characters, one of which is diagnostic for the species: instead of 2–4 spines, the basis of the female gnathopod 1 had 2–3 setae along the anterodistal margin (compare Fig. 3a with Fig. 7a and c). These setae had the same length as the spines they replaced and could be clearly distinguished from corre-

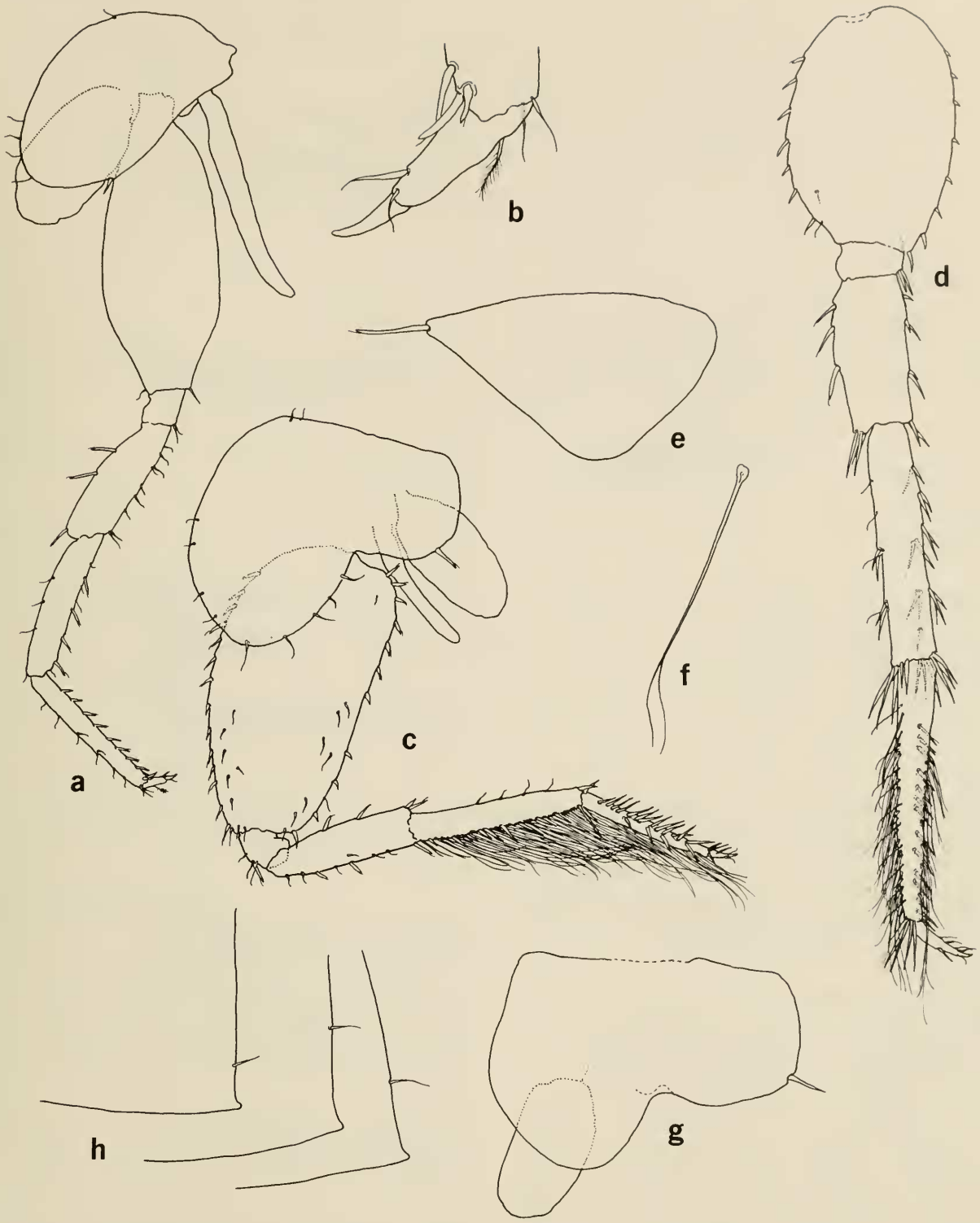

Fig. 4. *Spelaeogammarus spinilacertus* n. sp., allotype female: a) left pereopod 4, b) right pereopod 4 dactyl, c) left pereopod 5, d) right pereopod 7, e) coxal plate of right pereopod 7, f) bifurcate seta (on carpus and propodus of pereopod 5–7), g) coxal plate of left pereopod 6, h) epimeral plates.

sponding setae in *S. santanensis* and *S. trajanoae* (described below). Furthermore, both specimens (10 mm male and 7 mm female) had 3 subapical spines on each lobe of the telson. The male from the Jaburu sample also showed morphological variability in its appendages, e.g., the bases of both gnathopods and pereopods 3–6 were relatively narrow and elongate; similarly, the propods of both gnathopods appeared relatively longer and larger, with a conspicuously sinusoid palmar margin.

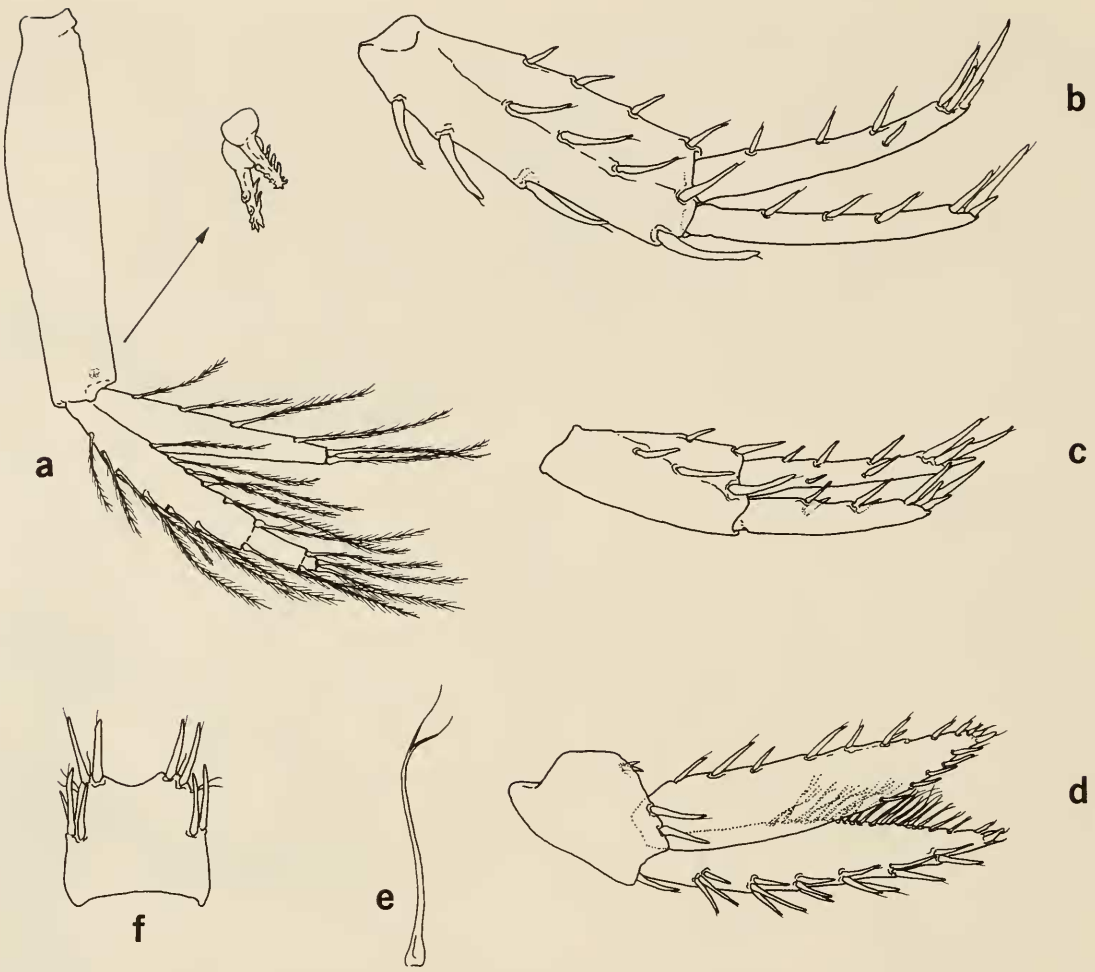

Fig. 5. *Spelaeogammarus spinilacertus* n. sp., holotype male: a) left pleopod 3, b) left uropod 1, c) left uropod 2, d) left uropod 3, e) bifurcate seta of outer ramus of uropod 3, f) telson.

Spelaeogammarus trajanoae, new species
Figs. 6b, i, 7c, d, 8a, b

Material examined.—Campo Formoso, Estado do Bahia, Brazil: holotype female (10.4 mm) and 5 paratypes (2 males, 3 females) from Toca do Pitu Cave (=Gruta do Pitu?), collected by A. Auler & M. Martins, Sep 1989; 1 male and 1 female paratype from Toca do Pitu Cave, collected by E. Rubbioli, Jan 1992; 3 paratypes (1 female, 2 juveniles) from Buraco do Teodoro Cave, collected by J. A. Cardoso (no date given); 1 female paratype from Toca do Gonçalo Cave, collected by P. Gernhard, 4 Jul, 1997; 1 fragmented specimen from Convento Cave, collected by S. Larizotti, 1986 (?).

The holotype is dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13341) and 2 paratypes from the type locality are deposited in the Museu Nacional. The allotype and the remaining paratypes are retained in the collection of the second author.

Diagnosis.—*Spelaeogammarus trajanoae* is morphologically closely allied with *S. spinilacertus* but can be distinguished from that species by 5–9 short setae instead of spines or spine-length setae on the distoanterior margin of the basis of gnathopod 1 and coxal plate 5 with approximately 18 setae plus 1 spine on margins instead of 9 setae plus 1 spine. Largest males 10.0 mm, largest female 10.5 mm. *S. trajanoae* is moreover distinguished from *S. spinilacertus* as indicated in the following description.

Description.—Antenna 1: Peduncular segment 1 with 5–7 spines; peduncular segment 2 with 3–4 short spines; peduncular segment 3 bearing 2 spines.

Lower lip (Fig. 6i) bearing setules on medial margin of outer lobes.

Maxilliped: Segment 2 with ±17 setae along medial margin. Inner and outer plate shown in Fig. 6b.

Gnathopod 1 (Fig. 7c): Posterior margin of basis bearing 9–10 singly inserted, long setae; anterior margin with 5–9 short setae. No setules on posterior margin of ischium. Carpus bearing 6–9 setae on pointed posterior lobe (4–6 comb-like and 2–3 naked). Palm of propodus even; lateral margin with 5–7 normal spines and 16–17 short bifid spines; medial margin with 6–8 short and 6 long setae.

Gnathopod 2: Posterior margin of basis with 8–9 long setae. Carpus posteriorly with 5–6 rows of setae (1–5 setae per row). Propodus with 6–8 rows of setae (1–3 setae per row) at proximoposterior margin; palmar margin with 3–4 lateral corner spines, 16–17 short lateral bifid spines, and 8–9 short medial setae.

Pereopods 3 and 4 (Fig. 8a): Basis bearing 1 spine at posterodistal margin; anterodistal margin sinusoid, with 1 spine and 1 seta (pereopod 3) or 2 spines and 1 seta (pereopod 4). Carpus bearing 6–7 spines posteriorly. Propodus with 13–15 spines along posterior margin.

Pereopod 5: Coxal plate with 17–18 marginal setae on anterior lobe. Anterior margin of basis bearing 10–12 spines; 15 short setae on both posterior and anterior lateral surfaces. Dactyl about 22% length of propodus.

Pereopod 6: Ischium with 2 spines and 1–2 setae. Dactyl about 26% of propodus length.

Pereopod 7: Basis with 11 spines on anterior margin and 10 spines on posterior margin. Merus with 3 sets of doubly inserted spines at posterior margin and 3 sets of spines at anterior margin (with 3–4 spines per set).

Pleopods: Outer ramus with 8–10 lateral plumose setae and 8–9 medial plumose setae on first segment. Inner ramus bearing 5–7 medial plumose setae.

Epimeral plates (Fig. 7d) with produced, bluntly rounded distoposterior corners.

Uropod 1: Peduncle with 3–4 spines on dorsolateral margin, 4–5 spines on dorsomedial margin. Inner ramus with 4–5 marginal spines, occurring as 4 dorsomedial and 0–1 dorsolateral spines.

Uropod 2: Peduncle with 1–2 dorsomedial spines, 2–3 dorsolateral spines.

Uropod 3: Outer ramus bearing 3–5 apical spines, 4–6 rows of spines (with 1–3 spines per row) along lateral margin. Inner ramus bearing 10–11 rows of spines (with 5 singly and 5 doubly inserted) at medial margin.

Telson (Fig. 8b) width about 81% of length, with u-shaped apical excavation (19% of length); each side with 3 apical setae, 2 apical spines, and 3–4 subapical spines.

Etymology.—The species is named in honor of Professor Dr. Eleonora Trajano of the University of São Paulo, who has made important contributions to Brazilian biospeleology.

Remarks.—Out of a total of 12 specimens examined, 2 individuals were found with 2 and 3 subapical spines on each telsonic lobe, respectively. The majority (10 specimens) had 4 subapical spines on one lobe and 3 subapical spines on the other lobe.

Spelaeogammarus santanensis, new species

Figs. 6a, e–g, 7a, b, 8c–e

Material examined.—Padre Cave, Santana, Estado do Bahia, Brazil: holotype male (13.6 mm), 3 male and 3 female paratypes (11.5–13.6 mm), and 1 juvenile paratype (10.6 mm), collected by F. Chaimowicz, July 1987.

The holotype is dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13342) and 2 paratypes are deposited in the Museu Nacional. The remaining paratypes are retained in the collection of the second author.

Diagnosis.—A comparatively large cavernicolous species, easily distinguished

Fig. 6. *Spelaeogammarus santanensis* n. sp., holotype male: a) inner and outer plate of maxilliped, e) detail of antenna 1, f) left mandible, g) detail of right mandible; *S. trajanoae* n. sp., paratype female (10.36 mm): b) inner and outer plate of maxilliped, i) lower lip; *S. spinilacertus* n. sp., holotype male: c) inner and outer plate of maxilliped; *S. bahiensis* paratype (8 mm juvenile): d) inner and outer plate of maxilliped, h) left incisor and lacinia mobilis.

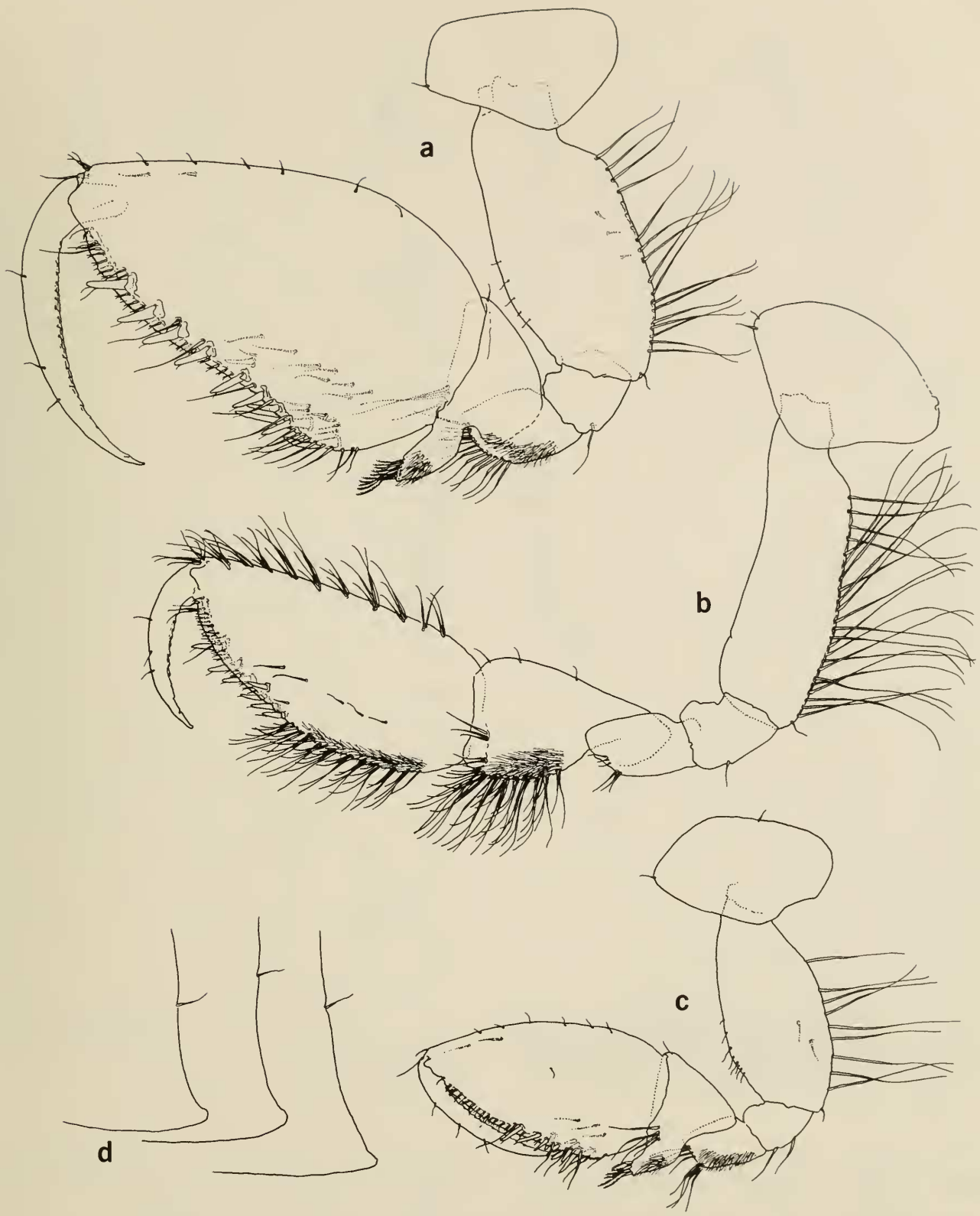

Fig. 7. *Spelaeogammarus santanensis* n. sp., holotype male: a) left gnathopod 1, b) right gnathopod 2; *S. trajanoae* n. sp., paratype female (10.36 mm): c) left gnathopod 1, d) epimeral plates.

from other species in the genus by having: 5-segmented accessory flagellum; 20–23 setae on posterior margins of the bases of gnathopods 1 and 2; propodus of gnathopod 1 proportionally larger. Largest male 13.6 mm, largest female 10.5 mm. *S. santanensis* is furthermore distinguished from *S. spinilacertus* according to the following description.

Description.—Antenna 1 about 40–45% length of body. Primary flagellum bearing 20–21 segments, some of which with mul-

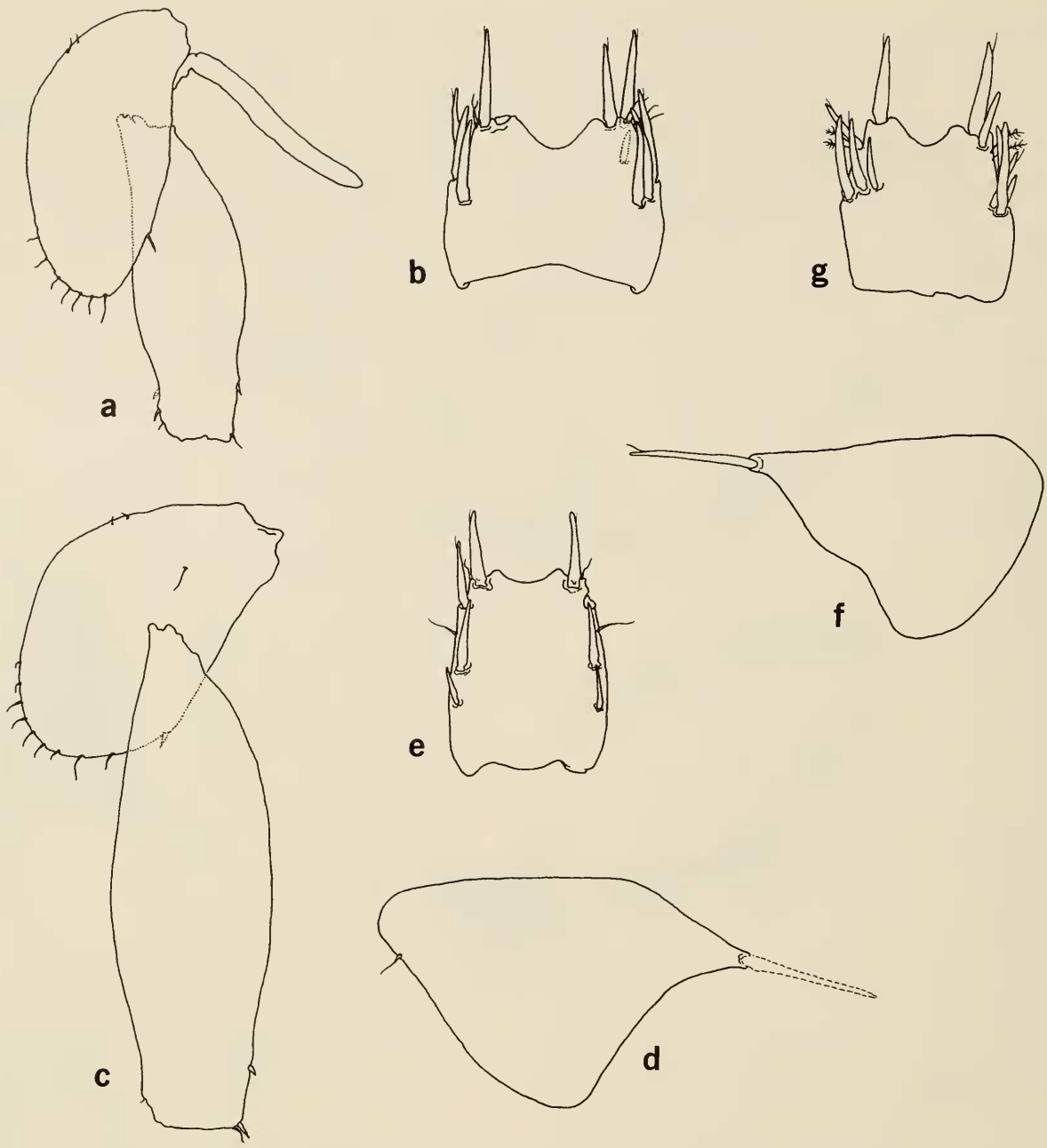

Fig. 8. *Spelaeogammarus trajanoae* n. sp., paratype female (10.36 mm): a) left pereopod 3, b) holotype female: telson; *S. santanensis* n. sp., holotype male: c) right pereopod 3, d) coxal plate of pereopod 7, e) telson; *S. bahiensis,* paratype (8 mm juvenile): f) coxal plate of pereopod 7, g) telson.

tiple inserted aesthetascs (Fig. 6e). Peduncular segment 1 with 5–6 spines; peduncular segment 3 with 2 ventromedial spines. Accessory flagellum 5-segmented.

Antenna 2 slightly shorter than antenna 1. Peduncular segment 5 with 5 ventral spines. Flagellum as long as peduncular segment 5, with 8–10 segments.

Mandible (Fig. 6f, g): Palp with 3 terminal setae. Palp segment 2 of left mandible with 3 setae and 1 spine; 3 short and 1(–2?) long plumose spines between lacinia and molar. Palp segment 2 of right mandible with 4 setae and 2 spines.

Lower lip with few thin setules on medial margin of outer and inner lobes; corner of outer lobes with slightly pointed corners.

Maxilla 1: Palp with 8–9 apical and subapical setae and a few lateral setules. Outer plate with 7 serrate spines apically.

Maxilla 2: Outer plate apically with 0–1 comb-like setae, ±21 plumose setae, and 1–2 plumose spines (slightly subapical). Inner plate bearing ±22 long comb-like setae and

several short naked setae (two of which on medial margin).

Maxilliped: Palp segment 1 with 2 medial and 2 proximomedial setae; segment 2 with ±25 medial setae; segment 3 bearing ±17 medial and 3 dorsomedial setae. Dactyl with 8 setae on outer margin. Inner and outer plate shown in Fig. 6a.

Gnathopod 1 (Fig. 7a): Posterior margin of basis bearing 20 long, singly inserted setae; anterior margin with 4 setae. Carpus with distinctly pointed posterior lobe, which bears 13–14 plumose setae. Propodus bearing 7–8 setae on medial surface; palmar margin sinusoid, with 10 short medial setae, 4 long lateral setae, 8–9 normal lateral spines, 19–20 short bifid lateral spines, 1 normal angular spine medially, 2–3 oblique subangular spines (1–2 relatively long), ±13 subangular lateral setae, and 6–7 subangular medial setae. Inner margin of dactyl with row of blunt denticles.

Gnathopod 2 (Fig. 7b): Posterior margin of basis bearing 21–23 long setae. Carpus posteriorly with 8–9 rows of setae and 5 short setae distolaterally. Propodus twice as long as broad; palm with 6 lateral spines and 1 medial spine, 18 short lateral bifid spines, 1 long lateral seta, and 12 short medial setae; palmar margin with blunt serration of whole margin, distinct serration and minute cilia at corner. Dactyl about 53% length of propodus, inner margin with row of blunt denticles.

Pereopod 3: Basis (Fig. 8c) with 2 spines at posteriodistal margin. Carpus bearing 5–6 spines posteriorly and 2–3 spines plus 1–2 setae anteriorly. Propodus with 11–12 spines along posterior margin (some doubly inserted) and 2 spines plus 4 setae apically. Dactyl about 25% length of propodus.

Pereopod 4 subequal to pereopod 3, except for the following differences: coxal plate with 1 spine and 8 setae along distal margin, 2 setae at proximal margin, and 3 setae on lateral surface. Basis with 2–4 spines at posterodistal margin.

Pereopod 5: Coxal plate with 12 setae on anterior lobe and 2 setae on lateral surface. Basis bearing 12 spines on anterior margin; anterior and posterior lateral surface with 4 short setae respectively. Ischium with 4 setae. Anterior margin of carpus with 5–6 sets of spines (2–3 singly and 2–3 doubly inserted). Lateral margin of propodus with 13 spines (5–6 doubly inserted). Dactyl about 18% length of propodus, bearing 1 plumose seta posteriorly.

Pereopod 6 subequal to pereopod 5 except for the following characters: coxal plate with 1 spine and 1 seta on anterior lobe. Basis without setae on posterolateral surface; anterolateral surface with 2–6 setae; posterior margin bearing 14 spines (pereopod 5: 11 spines). Merus posteriorly with 3 spines and anteriorly with 3–4 spines plus 3–4 setae (see *S. spinilacertus* for pereopod 5). Anterior margin of carpus with 8 spines (3 doubly inserted). Dactyl about 20% length of propodus, bearing 1 plumose seta and 1 spine posteriorly.

Pereopod 7: Coxal plate (Fig. 8d) irregular in shape. Basis with 10–11 spines on anterior margin. Ischium bearing 1 spine and 1–2 setae. Merus with 6 spines (3 doubly inserted) on anterior margin. Carpus with 3 sets of spines (with 3–4 spines per set) on anterior margin and 4 sets of spines (with 1–3 spines per set) on posterior margin. Anterior margin of propodus additionally with 10 sets of 1–3 slender spines. Dactyl about 21% length of propodus, with 1 plumose seta at posterior margin.

Pleopods: Outer rami bearing 12–13 lateral plumose setae and 7–8 medial plumose setae. Inner rami with 7–8 medial plumose setae.

Epimeral plates subquadrate, with small, subacute posterior margins, bearing 1 setule each.

Uropod 1: Peduncle with 4 spines on dorsolateral, 4 on dorsomedial, 3 on ventrolateral, and 3 on apical margin, respectively. Inner ramus with 7 dorsolateral spines (3–4 dorsomedial and 1–2 dorsolateral spines).

Uropod 2: Outer ramus bearing 4 dorsolateral spines (doubly inserted).

Uropod 3: Outer ramus bearing 2 spines

and 1 seta apically, 5 sets of spines (with 1–3 spines per set) along lateral margin; medial margin with ±8 bifurcate setae proximally and ±6 slender setae distally. Medial margin of inner ramus with 8 sets of singly and doubly inserted spines.

Telson (Fig. 8e) width about 76% of length; apex with shallow excavation (5% of length); each lobe bearing 1 spine plus 1 seta apically and 3 spines plus 1 seta subapically.

Etymology.—The proposed epithet *Santanensis* is a toponym, referring to the capital city Santana, which is situated near the type-locality.

Remarks.—In marked contrast to the 3 other species of the genus, the preserved specimens of *S. santanensis* appeared whitish and almost transparent. Specimens of *S. spinilacertus* and *S. trajanoae* were yellowish-grey, whereas *S. bahiensis* showed a dark, brownish tone. Since these variations appeared to be interspecific (i.e., consistent for species from different localities) it is possible that they were caused by structural differences of the exoskeletons.

Spelaeogammarus bahiensis da Silva Brum, 1975
Figs. 6d, h, 7f, g

Material examined.—Patamute Cave (type locality), Curaça, Distrito de Matamuté, Estado do Bahia, Brazil: 1 male paratype, 11.1 mm, and 1 juvenile paratype, 8 mm (Museu Nacional catalogue no. MN 5725), collected by P. Magalhães, 1972–1973 (?).

Diagnosis.—*Spelaeogammarus bahiensis* is morphologically more similar to *S. spinilacertus* and *S. trajanoae* than to *S. santanensis* but differs from the former two species in having 7 serrate spines on the outer plate of maxilla 1, 20–21 setae on coxal plate 5, and the presence of dorsal setules on pereonite 7 (1 setule), pleonites 1–3 (2–10 setules), and uronites 1–2 (1–7 setules). In addition, it is distinguished from *S. spinilacertus* by short setae instead of spines on the anterior margin of the basis of gnathopod 1. Male specimen 11.1 mm in length. Corresponding to the original description by da Silva Brum (1975) with the additions and modifications given below.

Redescription.—Antenna 1: Peduncular segment 1–3 gradually decreasing in length; peduncular segment 1 with 6 ventral spines. Aesthetascs on most segments of primary flagellum (as long as segments); accessory flagellum with 4 segments, terminal segment vestigial.

Antenna 2: Peduncular segment 3 with 3–4 spines. Flagellum with 7 segments.

Mandible: Left lacinia mobilis distinctly toothed. Long and short plumose spines between lacinia and molar more dissimilar than in other species (Fig. 6h).

Maxilla 1: Palp without lateral setules. Outer lobe with 7 apical spines (3 different types) and distinct row of setules at medial margin, subapically.

Maxilliped: Dactyl bearing 3–4 relatively long setae along inner margin. Inner plate bearing apically 2 bifid (y-shaped) spines; outer plate with 3 blade-like spines subapically and 2 strong setae apically (Fig. 6d).

Gnathopod 1: Posterior margin of basis with 7–9 long setae (all singly inserted); anterior margin bearing 3–5 short setae. Carpus with rectangular posterior lobe, bearing 3–5 long, sickle-shaped, naked setae, 3–6 comb-like setae, and 3–4 long, naked setae. Palmar margin of propodus bearing 5–9 normal spines and 13–18 short bifid spines on the lateral margin; medial margin with 8–10 short setae, 1 normal angular spine, and 3–5 corner spines (1–2 relatively long). Dactyl with 9–10 denticles, each with 1 short seta.

Gnathopod 2 basically like that of *S. spinilacertus*. Palp with 2 normal spines and 4 spines at corner. Dactyl with 6–7 denticles.

Pereopods 3 and 4 subequal. Pereopod 3 basis with 1 distoanterior spine, and 1 distoposterior seta. Pereopod 4 basis with 1–2 distoanterior spines and 1 seta plus 1 spine

at distoposterior margin; dactyl with 1 spine similar to *S. santanensis.*

Pereopods 5–7 missing in specimens examined.

Pleopods basically like those of *S. spinilacertus.* Segment 1 bearing 7–8 lateral plumose setae and 5–6 medial plumose setae. Inner ramus with 7 plumose setae on medial margin.

Coxal plates 3–4 with 9–10 setae and 1 spine; plates 5–6 identical, bearing 20–21 setae and 1 spine, respectively; plate 7 (Fig. 8f) irregular, slightly lobed.

Uropod 1: Peduncle with 4 spines on dorsolateral, dorsomedial, and ventrolateral margins, respectively, and 2 on apical margin. Outer ramus with up to 5 apical spines. All spines on inner ramus singly inserted.

Uropod 2: Peduncle bearing 1–2 dorsomedial, 1–2 dorsolateral, and 2 apical spines.

Uropod 3 missing in specimens examined.

Telson (Fig. 8g) width about 80% of length; each lobe bearing 2 setae, 2 apical and 3–4 subapical spines.

Discussion

The four species described above are recorded from eight caves in a series of discontinuous karst areas that extend over a linear distance of ca. 1200 km from north to south in eastern Brazil (Fig. 9). The records for each species per karst area are as follows: *S. santanensis*—1 cave, *S. bahiensis*—1 cave, *S. spinilacertus*—2 caves, and *S. trajanoae*—4 caves. Each species is obviously restricted to one or more caves in a separate karst area. These areas are disjunct and apparently physically isolated from each other. The greatest distance between caves with two species is roughly 650 km (*S. bahiensis* and *S. santanensis*), whereas the shortest distance is only about 135 km (*S. bahiensis* and *S. spinilacertus*). Caves situated within a single, continuous karst area that are inhabited by the same species are never more than ca. 100 km apart.

Both the elongate coxal plates and aequiramus pleopods found in the genus *Spelaeogammarus* are characters usually considered plesiomorphic for the family Bogidiellidae (Stock 1981, Barnard & Barnard 1983). Apart from *Spelaeogammarus,* coxal plates that are longer than wide are known only for the genus *Artesia* Holsinger, 1980 (*in* Holsinger & Longley 1980), and this genus, like *Spelaeogammarus,* also has pleopods with aequiramus inner rami. However, they are 5-segmented in *Artesia* and only 1-segmented in *Spelaeogammarus. Artesia* can also be distinguished from *Spelaeogammarus* by 1-segmented accessory flagellum, fewer flagellar segments in both antennae, 1-segmented palp of maxilla 2, 6-segmented pleopodal exopodite, unlobed coxal plates 5 and 6, and the telson, which is deeply cleft and bears 4–6 apical spines on each lobe. Equally long rami are also found in *Aequigidiella* Botosaneanu & Stock, 1989, *Kerguelenicola* Ruffo, 1974, and *Parabogidiella* Holsinger, 1980 (*in* Holsinger & Longley 1980). However, in these three genera the coxal plates are typically wider than long. Moreover, *Aequigidiella* differs from *Spelaeogammarus* by sexually dimorphic inner rami and spines of the second uropods of the male and a telson that is much longer than wide. Although to date only one specimen of the genus *Kerguelenicola* is known, there are several characters that distinguish it from *Spelaeogammarus:* 1-segmented accessory flagellum, distinct shape of and lack of armature on the telson, large mandibular molar, and reduced number of spines and setae on the outer and inner lobes of maxilla 1. *Parabogidiella* differs from *Spelaeogammarus* by 1-segmented accessory flagellum, 5-segmented flagellum of antenna 2, 1-segmented palp of maxilla 2, characteristically elongated pereopod 7, 5 pairs of coxal gills, and armature of the telson.

The most closely related bogidiellid taxon to *Spelaeogammarus* described to date may be *Bogidiella gammariformis* Sket (1985) from a cave in Equador. This species

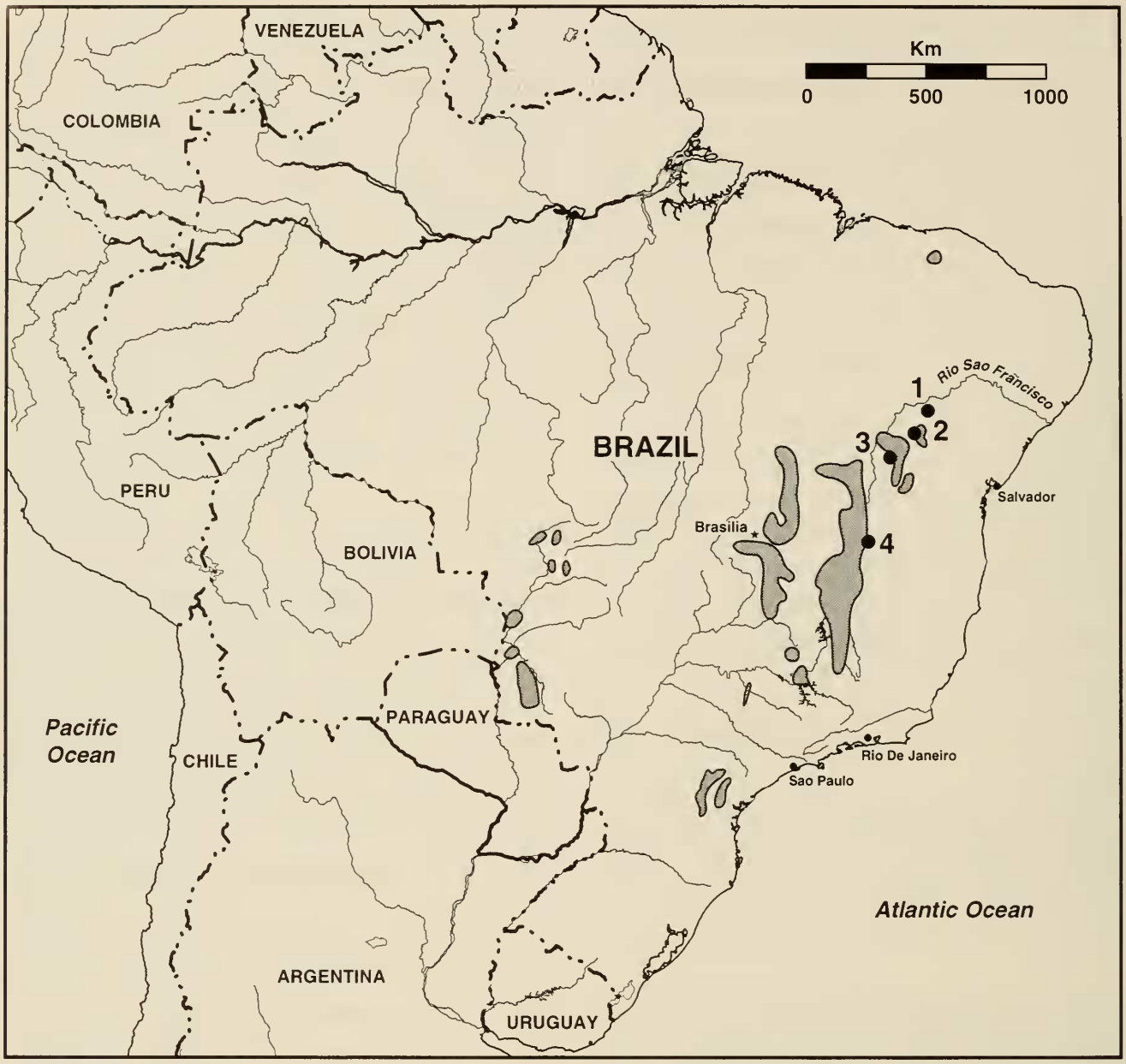

Fig. 9. Distribution of species of *Spelaeogammarus* in eastern Brazil: 1) *S. bahiensis* (1 cave); 2) *S. trajanoae* (4 caves); 3) *S. spinilacertus* (2 caves); 4) *S. santanensis* (1 cave). Shading indicates principal cave and/or karst areas. Map adapted from Trajano & Sanchez (1994).

features some interesting characters that might be interpreted as intermediate states between the relatively primitive *Spelaeogammarus* and the more derived *Bogidiella* s. str. For example, *B. gammariformis* has enlarged, bilobed coxal plates 5 and 6, which are longer than wide, therefore showing a strong resemblance to the coxae of *Spelaeogammarus*. The inner rami of the pleopods of *B. gammariformis* are also 1-segmented, but show the same reduction as in most other species of *Bogidiella* s. str. (i.e., shorter than segment 1 of the outer ramus).

The concentration of the four morphologically closely similar species of *Spelaeo-*

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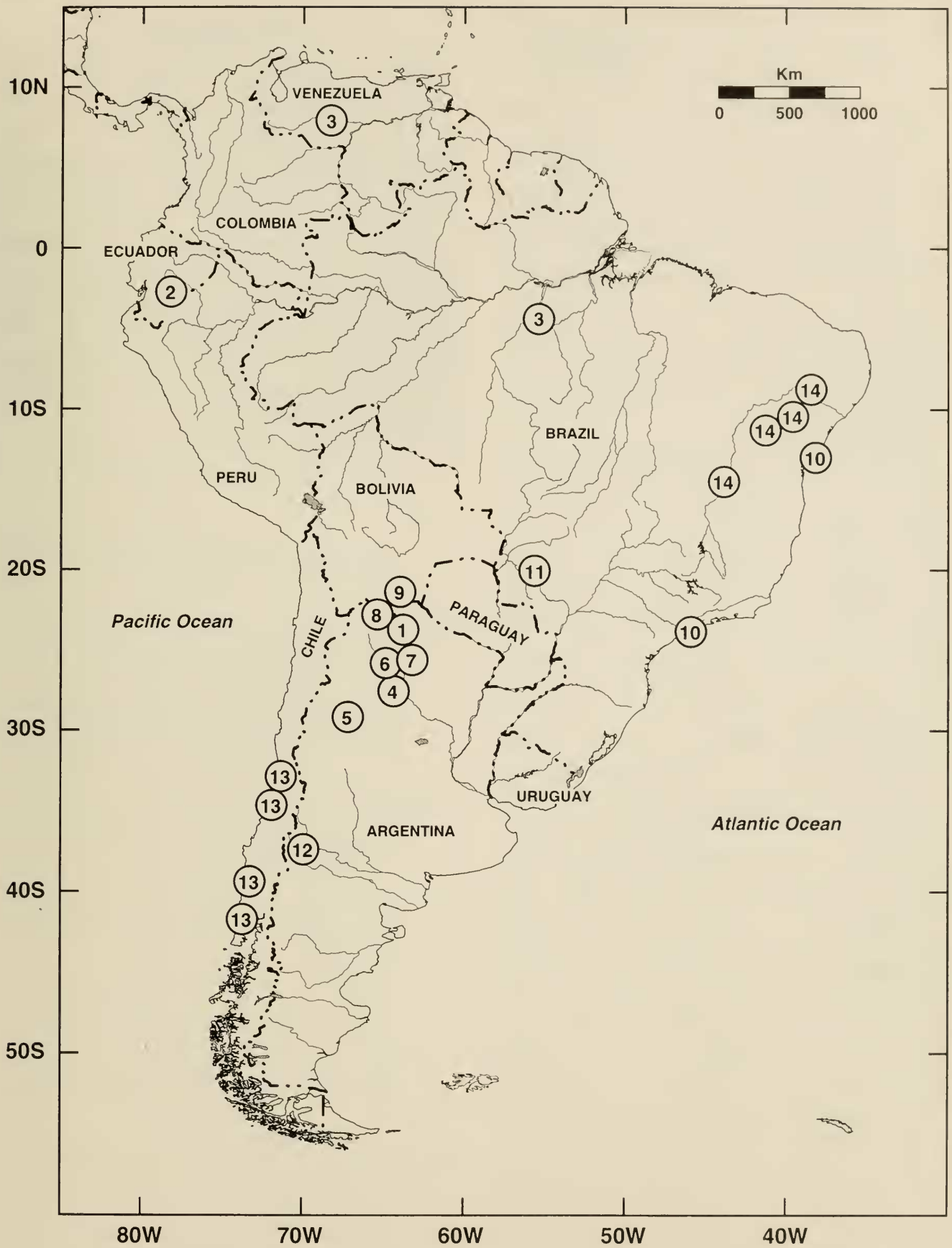
Fig. 10. Distribution of bogidiellid genera in continental South America: 1) *Bogidiella cooki* Grosso & Ringuelet, 1979; 2) *B. gammariformis* Sket, 1985; 3) *B. neotropica* Ruffo, 1952; 4) *B. (Dycticogidiella) ringueleti* Grosso & Fernandez, 1988; 5) *B. (Dyct.) talampayensis* Grosso & Claps, 1985; 6) *B. (Mesochthongidiella)*



tucumanensis Grosso & Fernandez, 1985; 7) *B. (Stygogidiella) hormocollensis* Grosso & Fernandez, 1988; 8) *B. (Styg.) lavillai* Grosso & Claps, 1984; 9) *Eobogidiella purmamarcensis* Karaman, 1982; 10) *Marigidiella brasiliensis* Stock, 1981; 11) *Megagidiella azul* Koenemann & Holsinger, 1999; 12) *Patagongidiella danieli* Grosso & Fernandez, 1993 and *P. mauryi* Grosso & Fernandez, 1993 (sympatric species); 13) *Pseudingolfiella chilensis* Noodt, 1965; 14) *Spelaeogammarus bahiensis* da Silva Brum, 1975, *S. santanensis* n. sp., *S. spinilacertus* n. sp., and *S. trajanoae* n. sp.

gammarus in a series of disjunct caves is unique for South America (see Fig. 10). Particularly interesting are the relatively subtle morphological differences between the four species that, in turn, appear to be correlated with the interspecific spatial distance as well as the abundance of species per area: *S. spinilacertus* and *S. trajanoae* occur in the central part of the range of *Spelaeogammarus* and show the highest morphological resemblance. In contrast are the more obvious differences between the relatively large *S. santanensis* and the smaller *S. bahiensis,* which occur on opposite ends of the generic range.

In South America there is a second concentration of species in northern Argentina, which occur exclusively in hyporheic (?) habitats along the Rio Grande (see Fig. 10). This cluster is also strictly endemic but it has a higher generic diversity, with six species in two genera and three subgenera, possibly reflecting the time of divergence from a very old freshwater precursor and the subsequent radiation into a region of isolated inland habitats. However, the distribution pattern of *Spelaeogammarus* seems to indicate quite a different historical scenario, inasmuch as the species of this genus show an exceptionally close morphological relationship with each other when compared with all other South American bogidiellids. If we assume, for the sake of argument, the same evolutionary rate for all South American bogidiellids, the cluster of species belonging to *Spelaeogammarus* appears to have originated from a common ancestor far more recently as opposed to other bogidiellids in South American freshwater habitats.

The morphological appearance of the four species as well as their distribution over a relatively wide range of disjunct karst "islands" characterize *Spelaeogammarus* as a distinct genus within the family Bogidiellidae. The apparent isolation of these species may well reflect a sequence of allopatric (geographic) speciation events over a relatively short period of time.

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